VEGETATION OF SAND DUNES AT WILSONS PROMONTORY, VICTORIA

D. H. Ashton[1] & Marion van Gameren[2]

[1]Botany Department, University of Melbourne, Parkville, 3052, Victoria, Australia

[2]Earthlines, 127 Victory Parade, West Heidelberg, 3084, Victoria, Australia

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Two adjacent parallel dune systems on the west coast of Wilsons Promontory differ in their $CaCO_3$ content and therefore their soil pH. The calcareous dunes are more species rich than the siliceous dunes and although the major species on both dune systems are similar, at least one species, (*Swainsona lessertiifolia*), appears to be calcicolous. The scrub on the stable dunes mostly consists of even-aged stands as a result of numerous past fires. In most stands on Norman Bay *Leptospermum laevigatum* is dominant and *Leucopogon parviflorus* sub-dominant. The proportion of these species in the vegetation is likely to depend on the age of the stand and the frequency and severity of fires and droughts. In old stands, *L. laevigatum* is senescent with little or no regeneration due to seed harvesting by ants and persistent browsing by mammals. By contrast, *L. parviflorus* is rarely browsed, is more shade bearing and fire tolerant and although it remains vigorous in old stands it is damaged by sustained drought. It is likely to become the stand dominant in the presence of herbivores and in the continued absence of fire and severe drought, or any other disturbance. In severe SW storms fine calcareous beach sand at Norman Bay, is winnowed out over the dune scrub for up to 200 m inland, may delay normal processes of podzolization.

Key words. Sand dunes, calcareous, scrub, regeneration

THE COAST of Wilsons Promontory is characterised by granitic headlands and wide, curved sandy beaches. The junction of two sand provinces in Bass Strait occurs at Wilsons Promontory (Bird 1976), hence yellowish, calcareous sands and shell fragments from the continental shelf to the west are deposited on the west coast whist white quartzose sands derived from the east and southeast are deposited on the east coast. Similar patterns are also found on King and Flinders Islands (Bird 1976). However on the west coast of Wilsons Promontory (Fig.1) the siliceous sands at Leonard Bay are an exception which Bird (1993) suggests may be due to the deflection of the westward drift of calcareous material by the Glennie Group of islands off-shore The two adjacent, contrasted beaches at Norman Bay (Fig. 2a) and Leonard Bay (Fig. 2b) provided a convenient locale to compare the types of sand dune vegetation and to investigate stand dynamics on the calcareous system (van Gameren (1977).

The recent geological history of the Tidal River area is complex. Shell beds dated at dated at 6230+/-350 Yr BP. (Parsons 1966) occur at Tidal River 1.6-1.7 km inland under peats dated at 4960 Yr BP (G.S. Hope, personal communication) and indicate the existence of an estuary prior to the development of parallel dunes and swampy peats. Siliceous parabolic dunes and sand sheets of probable Pleistocene age occur on the surrounding granitic slopes at Tidal River (Parsons 1966) and behind Leonard Bay, indicating a period of considerable instability.

Norman Bay is broad and gently shelving and the wide beach is backed by up to six parallel calcareous dunes and one landward siliceous dune (Parsons 1966). Leonard Bay is narrower and steeply dipping and is backed by a single large siliceous dune which is under attack by large storm waves (Fig. 3). Although the Norman Bay front dune is occasionally eroded by storm waves it has been colonized by pioneer plants, such as *Thinopyrum junceiforme, Spinifex sericeus* and the exotic, *Euphorbia paralias,* forming embryo dunes. Further back, patches of scrub consist of *Olearia axillaris, Ozothamnus ferrugeneum, Correa alba, Leptospermum laevigatum* and *Leucopogon parviflorus*. The parallel dune system at Norman Bay extends 200-300 m from the beach and the extensive scrub shows considerable variation in age and species richness. By contrast the parallel dune at Leonard Bay extends only 80-90 m from the beach and the scrub on the lee side is restricted and relatively species poor.

Leptospermum laevigatum regenerates copiously after fire or disturbance (Parsons 1966; Hazard & Parsons 1977) and also vigorously invades adjacent, unburnt heathland (Burrell 1981). However its regeneration in stands of mature and degenerating scrub is meagre or absent. Its status was therefore studied in terms of autecology and field sowing trials.

The climate of the area is mild and maritime with a seasonally well distributed rainfall of about 1000 mm per annum. In spite of this, dry years occur which result in damage to vegetation and an increased chance of fires. Most of the northern half of the Norman Bay system beyond 90 m from the beach has been modified to various extents for the general development of tourism.

The nomenclature of vascular species follows The Flora of Victoria (Walsh & Entwistle 1994-99), that of bryophytes follows Scott & Stone (1976).

METHODS

Sand, soils and vegetation of Norman and Leonard Bays

Transects were set up at both bays and extended inland normal from the coast. At various distances, soils were sampled from soil pits, pH was determined by glass electrode using a 1:5 dilution with distilled water. The $CaCO_3$ content of beach sand in 1960 was determined by Ms Mary Todd using 0.1M HCl followed by back-titration with alkali (Piper 1950). In 1986 sand size spectra were determined by sieving sand collected from 0-10 and 30-40 cm to a mesh of 0.25mm. The dry weight of sand fractions was obtained after organic matter had been destroyed by H_2O_2.

Species cover was qualitatively assessed on the Braun Blanquet scale of +-5 (Kershaw 1964) in quadrats (10 x 1m) perpendicular to the transect. Quadrats did not extend to the heathland at either bay.

Even-aged scrub stands at Norman Bay

The structure of different even-aged stands of *Leptospermum laevigatum* and *Leucopogon parviflorus* were studied by bisect profiles in 1972. The species composition of mature and immature scrub was assessed from 5 random quadrats (10 x 1m). The demography of the two dominants was assessed from 50 distance measurements using the wandering quarter method of Catana (1963). The comparative regeneration of *L. laevigatum* scrub following the wildfire in NE Wilsons Promontory 1963, was assessed from 10 quadrats at intervals of 1, 9 and 28 years after the fire. The size of quadrats was commensurate at each time with that of the vegetation.

Accretion of beach sand by mature scrub on stable dunes

In the mature scrub at Norman Bay appreciable quantities of fine sand were found to have been collected in the flakey bark, furrows and notches of *L. laevigatum* trunks 90 m from the beach and also in epiphytic moss cushions of *Tortula papillosa* and *Zygodon intermedius* on the stems of *L. parviflorus*. Sand was collected from mature *L. laevigatum* trunks and passed through a series of sieves down to a mesh of 0.1 mm and compared with a similar sand spectrum of adjacent top soil (0-2 cm and 10-12 cm) in the mature scrub and

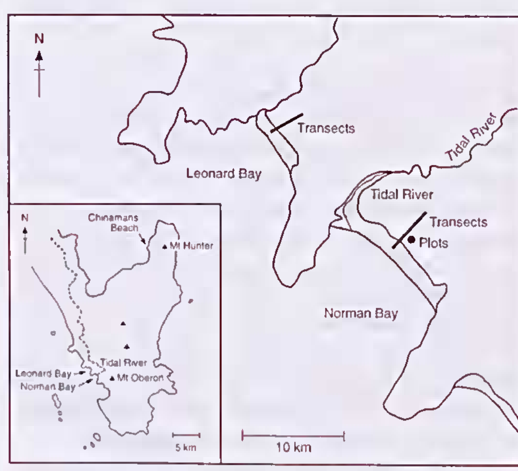

Fig. 1. Map of Wilsons Promontory, showing the location of the study sites.

Fig. 2. General view of dune systems. (a) Norman Bay and (b) Leonard Bay mid 1960s.

at intervals of 30 m as far as the beach. An indication of the rate of accretion of fine sand was obtained over a 7 month period from August 1999, by randomly placing nine plastic cups (9 cm diameter) on the soil surface in mature scrub 90-100 m from the beach, and in young scrub on the first dune 50 m closer the beach. After organic matter was destroyed, the dry weight of sand was expressed as g m^{-2} per month.

Regeneration of mature L. laevigatum scrub in the absence of fire

Sources of seed. In this area, abundant seed is stored in the canopy for up to one year after late spring flowering (Judd 1990) Seed fall was measured in suspended seed traps (Cunningham 1960); 5 being under canopy and 4 in gaps. Collections were made from April- October 1977, and seed counted and expressed as N° m^{-2}. Losses of seed from prepared soil surfaces (Ashton 1979) were assessed in May and August under mature scrub. In June 1977 the soil seed bank was investigated from ten plots (30 x 30 cm) at one cm intervals to a depth of 4 cm. Soil was sieved, moistened and incubated in a glasshouse for several months during which time all germinates were counted and identified. The germination of natural seed fall in eight random, 1 m^2 permanent quadrats under scrub canopy and in gaps was monitored from every 6 weeks from June-October 1977. The number of seedlings m^{-2} of both dominant species were calculated each month.

Fig. 3. Flakey bark of *Leptospermum laevigatum* where sand collects (right) and the rugose bark of *Leucopogon parviflorus* which supports epiphytic mosses which also collect fine sand (left).

Seed germination requirements. These were studied in the laboratory using a range of controlled temperatures (3-26° C), various light conditions (light, dark and a 12 hour photoperiod) and stratification storage periods of 4-8 weeks. In addition, seed was pricked with a fine needle to discover the existence of seed hardedness. Germination for each experiment was set up in 5 petri dishes using 0.25 g of seed for each treatment (1g contains 874 viable seed).

Fenced sowing trials. Natural gaps were deemed the most likely sites for successful regeneration. Three such gaps 5 m in diameter were found in the mature scrub area from crest to swale, 90-100 m from the beach. In June 1977 a plot (3.7 x 2.9 m) was fenced with wire mesh (2 cm diameter and 1.5 m high) in each gap. An adjacent unfenced plot acted as a control. Herbaceous material was removed and within each plot two blocks of of sub-plots (60cm^2) was set up in which the light litter layer was either removed or left intact. Seed sown at the rate 1 g per treatment. Germination and survival monitored at frequent intervals in the first year and at progressively longer intervals over the ensuing 20 years.

The effect of drought on scrub dominants

Following marked damage of dune scrub by drought in 1975, the degree of water stress of *L. laevigatum* and *L. parviflorus* was assessed in the field by determining the water potentials of shoots using the pressure-bomb method (Tyree and Hammel 1972). The relationship between water potential and relative water content of drying shoots was obtained in the laboratory.

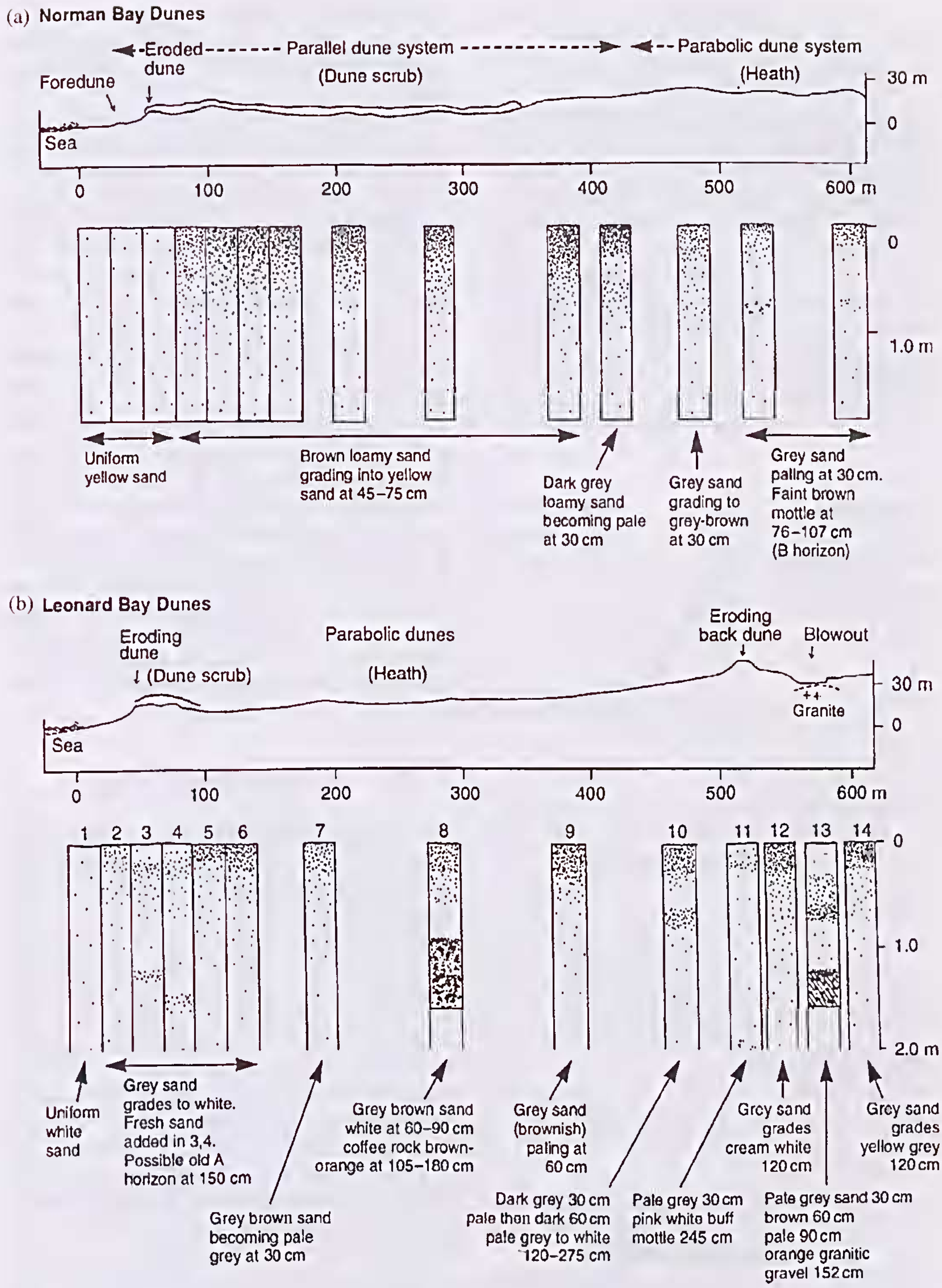

Fig. 4 Land profile of a) the Norman Bay dunes and b) Leonard Bay dunes.

RESULTS

Comparison of the two bay's dune systems

The most important difference in the two bays is the color and characteristics of the beach sand, the percentage of $CaCO_3$ and the consequent pH of the dunes that have been produced. At Norman Bay the pH of the beach sand is 8 and contains 34% $CaCO_3$ whilst at Leonard Bay the pH is 7 and contains only 0.4 % $CaCO_3$. The pH of dune soil at Norman Bay remains high and decreases slowly with distance inland for 200 m after which it falls to about 6. At Leonard Bay however the pH decreases quickly to 5.5 (Fig 5) The sand fraction data indicate that Norman Bay beach and parallel dunes are made of very fine sand (mostly 0.11-0.16 mm) whilst Leonard Bay the substrate is coarser fine sand (mostly 0.25-0.53 mm) (Fig. 6). The frequency spectrum of sand collected by vegetation was almost indistinguishable from that of dune and beach sand.

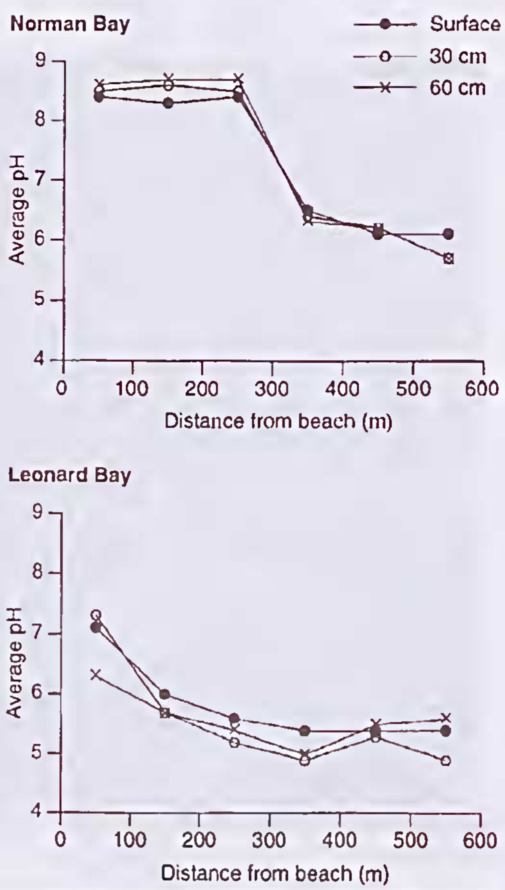

Fig. 5 The pH of soil with increasing distance from the beach at a) Norman Bay and b) Leonard Bay

The distribution of species on the two dune systems shows both similarities and differences (Table 1). The scrub on both dune systems is dominated by *L. laevigatum* and *L. parviflorus* and some *Allocasuarina verticillata* and *Correa alba*. The annual, *Daucus glochidiatus* is ubiquitous in winter. The species richness as indicated from transect quadrats, is much greater on the calcareous dunes (41 spp) than on the siliceous dunes (24 spp). The similarity index (2 x N° spp in common as a % of the sum of species in both stands) is 63%. Species restricted to the calcareous dunes include *Bursaria spinosa, Senecio biserratus* and *Swainsona lessertiifolia, Caladenia latifolia, Lagenophora stipitata* and the mat moss, *Thuidium laeviusculum*. Although *Exocarpos syrticola, Calocephalus brownii* and *Dianella revoluta* are common on the acid dumes at Leonard Bay, they may also be found elsewhere on calcareous soils. Occasional shrubs found more frequently on heath (*Grevillea lanigera, Hibbertia sericea, Spyridium parvifolius, Epacris impressa* and *Astroloma humifusum*) occur in more open areas of dune scrub at Leonard Bay and on the parallel, siliceous acid dune inland from Norman Bay.

Even-aged stands of dune scrub at Norman Bay

The vegetation on the stable dunes at Norman Bay ranging from dense, young *L. laevigatum* stands with little undergrowth and a trunk-space filled with criss-crossed dead branches, to old degenerating mature stands with gnarled, prostrate *L. laevigatum*, bushes of *L. parviflorus, Correa alba, Bursaria spinosa, Phyllanthus gunnii*, scramblers such as *Clematis microphylla and Muehlenbeckia adpressa* and *Rhagodia candolleana*. An herbaceous stratum of *Senecio biserratus, Swainsona lessertiifolia, Dichondra repens, Parietaria debilis* and numerous orchids and mosses is conspicuous, particularly in the moister swales. On the partially eroded front dune, the scrub is patchy and wind-contorted. Stringers of sand blown in from the beach through breaks in vegetation are colonized by foredune species such as *Spinifex sericeus*, and *Euphorbia paralias*.

The even-aged stands frequently have sharp boundaries (Fig. 7) and are almost certainly the result of post-fire regeneration. At Lawsons Creek, NE

Wilsons Promontory, a severe fire in 1962 killed mature stands of *L. laevigatum*. One year later, the seedling regeneration was exceedingly dense(1204 +/-138 m^{-2}) and compared with capsules of the fire-moss, *Funaria hygrometrica* both in size and density. Nine years later the mean height of the young stand was about 2 m and the density was reduced by 90%. After a further 11 years the density had reduced to less than one fiftieth (22.9 m^{-2}) of that in 1963, while the mean height of dominant plants had doubled to 4 m (Fig. 8).

At Norman Bay, the density of the woody species and the floristic composition in young and old stands is shown in Tables 2 and 3. In general, the number of species increased with age of the stand. In some places where the exotic grass *Ehrharta erecta* had established vigorously, the richness of the ground flora was diminished- affecting especially, small orchids, (*Caladenia carnea, C. latifolia, Acianthus caudatus*

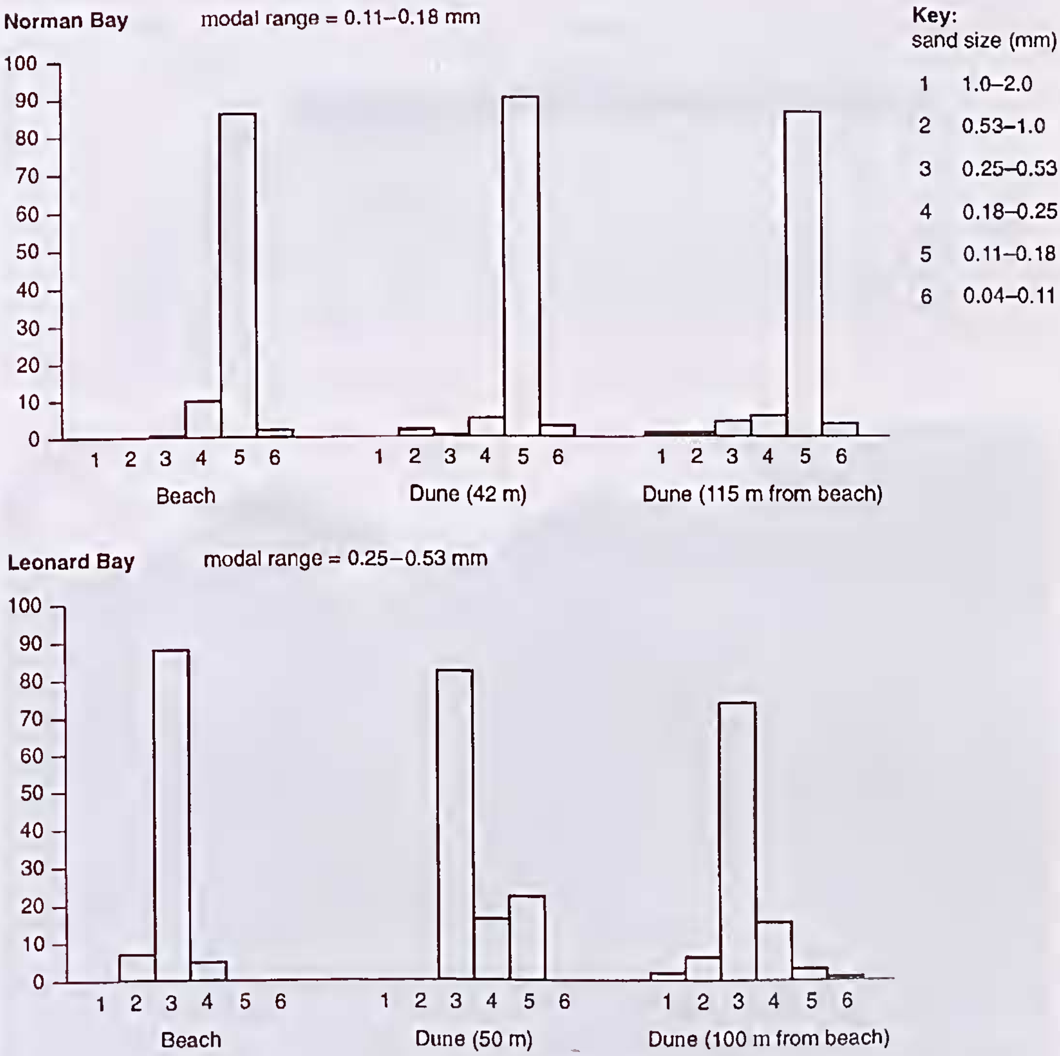

Fig. 6. Frequency histograms of sand size distribution of top soil with increasing distance from the beach at Norman Bay and Leonard Bay 1986.

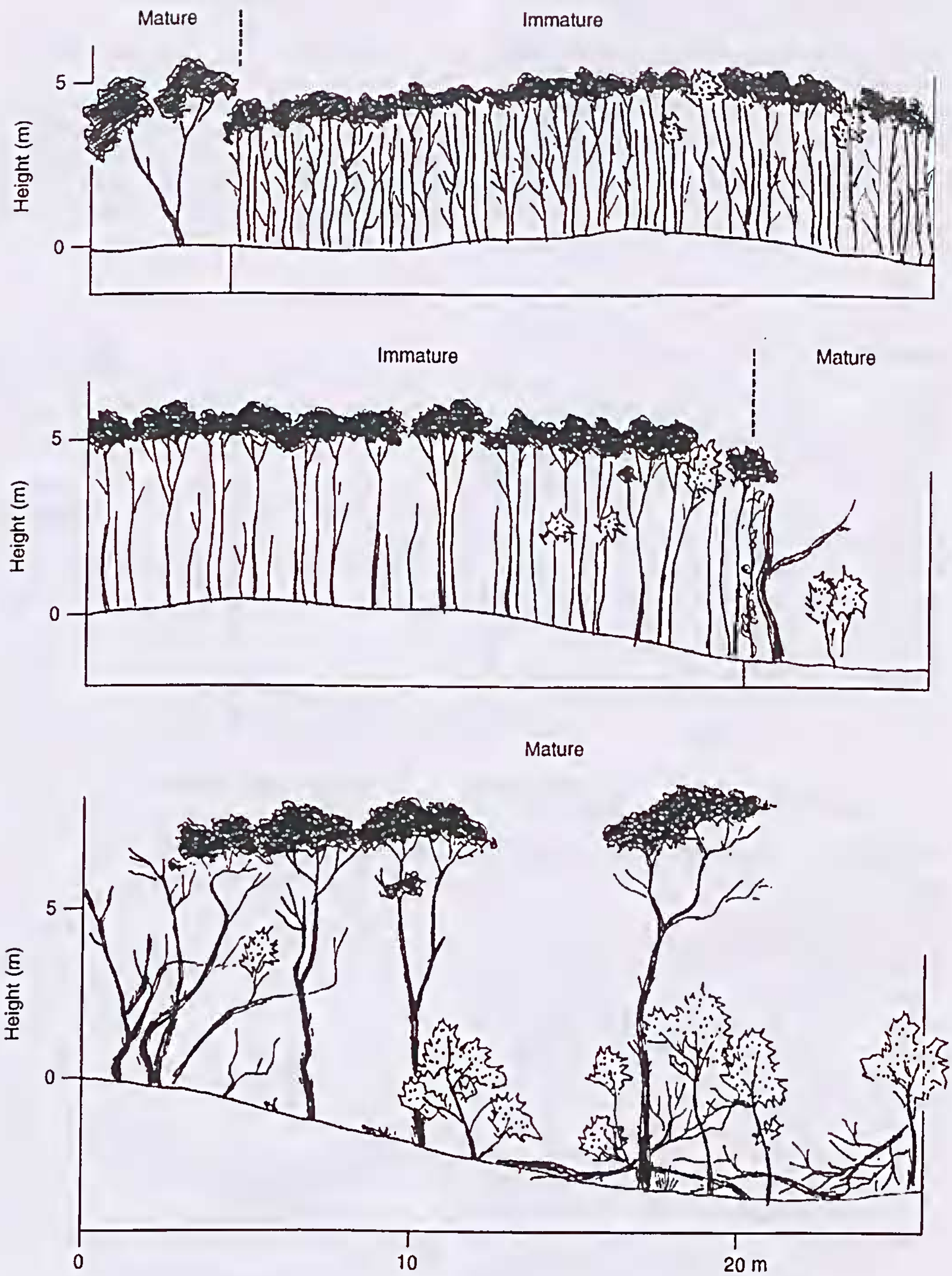

Fig. 7. Profiles of various even-aged stands of *L. laevigatum* at Norman Bay, 1972.

and *A. pusillus*) and ephemerals (*Daucus glochidiatus* and *Parietaria debilis*).

Although *L. laevigatum* is killed outright by fire, *L. parviflorus* resprouts from the butt or from buds below ground. Its growth appears to be slower than that of *L. laevigatum* and in immature stands it tends to be suppressed or subdominant. In old stands however, it becomes more vigorous as *L. laevigatum* senesces and is damaged progressively by severe storms. In contrast to *L. laevigatum*, *L. parviflorus* regenerates readily by seed in the mature stands and appears to be much less browsed.

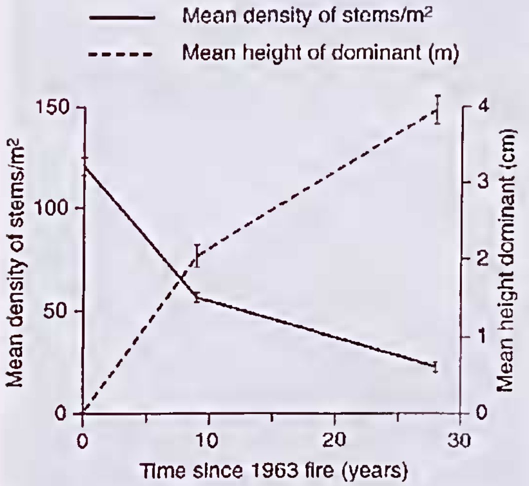

Fig. 8. Mean density and height of *L. laevigatum* regeneration at Chinaman Beach following the fire in NE Wilson's Promontory in 1962.

Regeneration of mature scrub in the absence of fire

Seed sources and germination requirements of L. laevigatum. The seed of *L. laevigatum* is small and fine (2.0 x 0.5 mm) with a potential viability of 91%. In the laboratory, germination is inhibited at 3°C and above 26°C but is optimal from 11°-16° C with 80% germination, when under a 12 hr photoperiod regime. The rate of germination is increased by pricking the seed coat and by stratifying for several weeks at 2-4°C. In the field, natural germination occurs between May and September when average maximum temperatures are in the optimal range.

In this area, capsules are stored in the canopy for up to 12 months from late spring flowering. Mean

Fig. 9. Photograph of fenced plot in a gap after 11 years, showing density and height of *L. laevigatum*. (Scale: Alan Andersen 1.9 m).

Fig. 10. Dead *L. parviflorus* (pale) amongst living *L. laevigatum* in the drought of summer 1976.

Species	Norman Bay (calcareous)										Leonard Bay (silicious)			
Distance from beach (m)	**3**	**10**	**32**	**42**	**85**	**100**	**135**	**160**	**175**	**200**	**5**	**40**	**60**	**80**
Shrubs, climbers														
Leptospermum laevigatum	·	·	1	1	+	1	2	2	1	2	·	+	3	3
Leucopogon parviflorus	·	·	+	1	1	1	1	1	1	1	·	·	2	2
Allocasuarina verticillata	·	·	·	·	1	·	·	·	·	·	·	·	·	·
Ozothamnus turbinatus	·	·	1	·	·	·	·	·	·	·	·	·	·	·
Olearia axillaris	·	·	1	·	·	·	·	·	·	·	·	·	·	·
Correa alba	·	·	2	+	+	·	·	·	·	·	·	1	·	·
Rhagodia candolleana	·	·	+	·	1	2	+	1	·	·	·	2	·	·
Tetragonia implexicoma	·	·	·	1	1	1	2	+	3	2	·	+	·	·
Clematis microphylla	·	·	+	1	1	+	+	+	+	+	·	·	·	·
Phyllanthus gunnii	·	·	·	·	·	·	1	·	·	·	·	·	·	·
Bursaria spinosa	·	·	·	·	·	·	+	+	+	·	·	·	·	·
Exocarpos syrticola	·	·	·	·	·	·	·	·	·	·	·	1	1	2
Calocephalus brownii	·	·	·	·	·	·	·	·	·	·	+	1	+	·
Grevillea lanigera	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Spyridium parvifolium	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Muehlenbeckia adpressa	·	·	·	·	·	·	·	·	·	·	·	1	·	·

Table 1. Species composition along transects normal to coast from high tide. Plots 10x1m at intervals (m). Cover estimated by Braun Blanquet scale: + (<1%), 1 (1-5%), 2 (5-25%), 3 (25-50%), 4 (50-75%), 5 (75-100%). * introduced.

Species	Norman Bay (calcareous)										Leonard Bay (siliceous)			
Distance from beach (m)	3	10	32	42	85	100	135	160	175	200	5	40	60	80
Hibbertia sericea	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Forbs														
Euphorbia paralias *	+	3	·	+	·	·	·	·	·	·	·	·	·	·
*E. peplus**	·	·	+	·	+	+	+	+	·	·	·	·	·	·
Senecio elegans *	·	·	+	+	·	·	·	·	·	·	·	+	·	·
S. lautus	+	·	+	+	1	·	·	·	·	·	·	+	+	+
S. biserratus	·	·	·	+	+	+	+	+	+	·	·	·	·	·
Cakile maritima	·	+	·	·	·	·	·	·	·	·	·	·	·	·
Sonchus asper *	·	+	·	·	·	·	·	·	·	·	·	·	·	·
S. oleraceus *	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Carpobrotus rossii	·	+	+	+	·	·	·	·	·	·	·	+	·	·
Galium sp.	·	·	+	+	·	·	·	+	·	·	·	·	+	·
Swainsona lessertiifolia	·	·	+	+	+	+	+	1	+	·	·	·	·	·
Daucus glochidiatus	·	·	+	+	+	+	+	+	+	+	·	1	+	+
Cynoglossum suaveolens	·	·	·	+	·	·	+	·	·	·	·	+	+	+
Dichondra repens	·	·	·	+	+	+	·	1	+	+	·	·	·	·
Parietaria debilis	·	·	·	+	+	+	+	·	+	+	·	·	·	·
Melilotus indica *	·	·	·	·	·	·	·	+	·	·	·	·	·	·
Hydrocotyle sp.	·	·	·	·	·	·	·	+	1	·	·	·	·	·
Lagenophora stipitata	·	·	·	·	·	·	·	+	+	·	·	·	·	·
Centaurium erythraea *	·	·	·	·	·	·	·	+	·	·	·	·	·	·
Oxalis corniculatus	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Crassula sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	+
Acaena anserinifolia	·	·	·	·	·	·	·	·	·	·	·	+	·	·
Monocotyledons														
Thinopyrum junceiforme	2	+	1	+	·	·	·	·	·	·	+	·	·	·
Ammophila arenaria	·	·	1	·	·	·	·	·	·	·	·	·	·	·
Lepidosperma gladiatum	·	·	+	·	·	·	·	·	·	·	·	·	·	·
Isolepis nodosa	·	+	+	·	+	+	·	·	·	·	·	1	+	+
Poa sp.	·	·	·	+	·	·	·	·	·	·	·	·	·	·
Lagurus ovatus	·	·	1	1	+	·	·	+	·	·	·	·	·	·
Carex inversa	·	·	·	·	·	·	·	+	·	·	·	·	·	·
Caladenia latifolia	·	·	·	·	·	+	+	+	+	+	·	·	·	·
Dianella revoluta	·	·	·	·	·	·	·	·	·	·	·	+	+	·
Lomandra filiformis	·	·	·	·	·	·	·	·	·	·	·	·	+	·
Cryptogams – Mosses														
Thuidium laeviusculum	·	·	·	1	+	2	3	2	1	+	·	·	·	·
Tortula princeps	·	·	·	+	·	·	·	·	·	·	·	·	·	+
Tortella calycina	·	·	·	·	+	+	·	+	·	·	·	·	·	·

Table 1. cont.

seedfall in May was 1400 m^{-2} under canopy and 25 m^{-2} in gaps 5 m in diameter, but in the ensuing four months this was reduced by 20-55%. Total yearly seedfall is likely to be adequate for regeneration. Long term storage of seed in the soil seems unlikely since in winter 1977, 91% of all germination was recorded from the upper 1 cm suggesting that it was derived from current seedfall.

Losses of seed from the soil surface were very high (90% in 24 hours) in May but were nil in August. Ants were observed taking *L. laevigatum* seed into their nests. The natural germination recorded from permanent quadrats over the period April to October 1977 was very low, viz: 1.0 m^{-2} under canopy and 0.75 m^{-2} in gaps.

Regeneration sowing trials. Initial germination 5 weeks after sowing was 84-100% of that predicted from the number of viable seed sown. After 4.5 months, mean survival inside fences was 15.1% of initial germination, whereas outside the fences it was 0.9%. Variability between blocks and plots was very high, hence although mean survival on bare soil and litter was 20.8% and 9.4% respectively, the difference was not statistically significant. Growth was slow and seedlings were only 1-2 cm tall at this time. After 3 years regeneration in the fenced plot was relatively

Species	Scrub	
Shrubs and climbers	Immature	Mature
Leptospermum laevigatum	*5 (4)*	*3 (2)*
Leucopogon parviflorus	*2 (+)*	*4 (+)*
Allocasuarina verticillata	*1 (+)*	*1 (+)*
Correa alba	*1 (+)*	*2 (1)*
Rhagodia candolleana	*3 (+)*	*2 (+)*
Tetragonia implexicoma	*2 (+)*	*4 (2)*
Clematis microphylla	*4 (+)*	*5 (+)*
Forbs		
Daucus glochidiatus	*4 (+)*	*5 (+)*
Parietaria debilis	*3 (+)*	*3 (+)*
Dichondra repens	*5 (+)*	*3 (+)*
Lagenophera stipitata	*2 (+)*	*2 (+)*
Senecio biserratus	·	*2 (+)*
Solanum *sp.*	*1 (+)*	·
Sonchus oleraceus *	*1 (+)*	*2 (+)*
Stellaria media *	·	*3 (+)*
Swainsona lessertiifolia	*2 (+)*	*2 (+)*
Viola hederacea	·	*5 (+)*
Caladenia latifolia	*4 (+)*	*4 (+)*
Centaurium erythraea *	·	*2 (+)*
Cynoglossum suaveolens	·	*1 (+)*
Graminoids		
Poa sp.	3 (+)	2 (+)
Lagurus ovatus	·	2 (+)
Bryophytes		
Thuidium laeviusculum	5 (+)	5 (1)
Tortula princeps	3 (+)	4 (+)
Lophocolea sp.	·	1 (+)
No. species	18	24

Table 2

Frequency and cover value(s) of species in immature and mature scrub, Norman Bay, 1984.

Five plots (10x1m). Cover values: + (<1%), 1 (1-5%), 2 (5-25%), 3 (25-50%), 4 (50-75%), 5 (75-100%). * introduced.

dense (up to 38 per plot), whereas outside the fences survival was nil. Two of the fenced plots were broken into after 4-5 years and all seedlings were stripped and killed. After 11 years the bushes in the remaining plot were capsule-bearing and vigorous (Fig 9), and after 22 years had reached heights of 8-9 m. Outside the were fences impenetrable thickets of *Bursaria spinosa* had developed- no doubt as a result of their effective physical defence against browsing to heights of at least 2 m. In the first year of the trial, it is likely that animal and/or bird scratching could have decimated unprotected germinates. Activity by wombats (*Vombatus ursinus*) was considerable around the plots. Browsing of larger seedlings could have been due to these animals as well as wallabies (*Wallabia bicolor*), European rabbits (*Oryctolagus cunnuculus*) or hog deer (*Cervus porcinus*). *Correa alba* and *Rhagodia candolleana* seedlings were also severely browsed but many other species such as *Leucopogon parviflorus, Phyllanthus gunnii* and the herbs, *Senecio biserratus* and *Swainsona lessertiifolia* were untouched and were probably unpalatable.

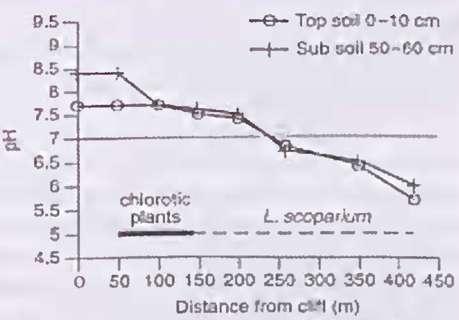

Fig. 11. Water potential (-bars) in shoots of *Leptospermum laevigatum* and *Leucopogon parviflorus* in relation to relative water content (% maximum uptake) in a severedrought, March 1976.

The effect of environmental stresses on the two dominant shrubs. *Leptospermum laevigatum* and *Leucopogon parviflorus* is different. In both 1975-76 and 1991-92 severe drought in this area resulted in yellowing and considerable foliage and branch death of both these species. In each case damage of *L. parviflorus* was considerably greater than that of *L. laevigatum* and sometimes resulted in the death of the whole shrub (Fig. 10). In early March 1976 the pre-dawn water potentials of shoots of *L. parviflorus* (-1.88 mPa) was significantly lower than that of *L. laevigatum* (-1.32 mPa)($t = 2.58$, $p<0.05$) for 5 replicates, indicating a greater degree of water stress in the former species. During a drying cycle of cut shoots the water potential of *L. parviflorus* was consistently lower than that of *L. laevigatum* for given relative leaf water contents (the water content as a percentage of maximum)(Fig. 11). Excavation of soil profiles revealed that in general, the roots of *L. parviflorus* were concentrated in the top half metre of soil whereas those of *L. laevigatum* were distributed more evenly and to a greater depth

DISCUSSION

The two adjacent dune systems are different in size, complexity and species composition. The beach sands are either very rich in $CaCO_3$ (yellowish) or very low (white) and the dunes which develop from them are therefore either acid or alkaline. Leonard Bay being steeply dipping, allows high energy waves at high tide to actively attack dunes. Norman Bay on the other hand shelves gradually and the beach is very wide and, although high tides and storms can result in dune attack, the recent environment has been conducive to foredune build up. Since air movement at ground level in dense

Scrub stage	Species	Density(No ha^{-1})	Mean Ht.(m)	Mean Girth at 30cm (cm)
Immature	*Leptospermum*	11991	4.6	16.3
	Leucopogon	3280	2.8	5.7
Mature	*Leptospermum*	5253	7.5	29.5
	Leucopogon	5016	2.5	9.2

Table 3. Comparitive stature of *Leptospermum laevigatum* and *Leucopogon parviflorus* in mature and immature scrub, Norman Bay dunes, 1984

dune scrub is slight- even during storms, it is considered that the very fine sand caught by bark and epiphytes 90 m inland has been derived from aerial transport from the beach Without doubt, the amount deposited in any year will be determined by the frequency and strength of onshore W-SW winds. It is possible that the fineness of the sand texture at Norman Bay is a major factor allowing such movement inland. Although the amount detected in cups in 1999-2000 was not great, a continual dusting of fine calcareous sand from the beach over decades or centuries could ameliorate normal podzolizing processes to some extent. The parallel dune systems are younger than the acid parabolic dunes and sand sheets in the hinterland where deep humus podzols are now developed (Parsons 1966).

In both dune systems the dune scrub of *L. laevigatum* and *L. parviflorus* is a relatively stable stage of development. The scrub on the Leonard Bay front dune is relatively poor in species and open areas are vegetated by conspicuous cushions of *Calocephalus brownii*. The more extensive scrub at Norman Bay is richer in species, certain of which (*Swainsona lessertiifolia*), are confined to the calcareous dunes. It appears to be a calcicole since it occurs on similar soils at both Yanakie Isthmus and Point Nepean. On the acid dune at Leonard Bay some of the heathland sclerophylls which occur in more open areas of scrub, may be calcifuges. The scrub on the Norman Bay dunes is composed of stands of different ages which are almost certainly related to past fires. Seedling regeneration of *L. laevigatum* following fire can be extremely prolific and thinning out of seedlings occurs very rapidly in the first few years. *L. laevigatum* eventually becomes senescent and prone to opening-up by storm damage. After 30 years the young stand studied in 1972 at Norman Bay had matured and the old stand had become moribund with many leaning and fallen stems of *L. laevigatum*. However the associated sub-dominant, *L. parviflorus*, had increased in both stature and cover and the diversity of the ground stratum had increased- probably as a result of increased light and soil moisture. Contrary to earlier years, occasional seedlings of *L. laevigatum* could be found in a few gaps, possibly as a result of the protection afforded by debris, tall herbs (such as *Senecio biserratus*), or from a decrease in the numbers of herbivores following rabbit control measures. The general lack of *L. laevigatum* regeneration in previous decades was not due to lack of seedfall but probably to a reduction of seed supply available for germination combined with summer droughts and severe browsing of established seedlings. It seems likely in previous decades, that the generally clear understorey and floor has enabled browsing animals to effectively control regeneration of palatable species. A corollary of this argument is provided by the massive invasion of dense heathland by *L. laevigatum* where the visibility of seedlings to herbivores such as swamp wallabies is impeded. *L. laevigatum* is fire-sensitive and easily killed. If fire occurs in its first 5 years, before seed has been produced, this species may be eliminated from a site. If fire does not occur for very long intervals and herbivore populations are high this species may not regenerate adequately. In some respects its ecology is similar to that of wet eucalypt forest species (Ashton & Chinner 1999).

Germination of *L. laevigatum* occurs in the cooler wetter months of the year but early growth is very slow and in dry years great losses could have occurred in spring and summer. After fire *Leucopogon parviflorus* usually regenerates from buds at or below ground level as well as from seed. It is dispersed actively by birds. As the stand matures *L. parviflorus* increases in prominence and in senescent stands may comprise much of the canopy. Without the intervention of fire stands of dune scrub at Wilson's Promontory are likely to become increasingly dominated by *L. parviflorus* -

Favouring factor			
Fire	*L. laevigatum*	¬	*L. parviflorus*
Very frequent fire < 5 yrs	*L. laevigatum*	®	*L. parviflorus*
No fire for 50-100 years	*L. laevigatum*	®	*L. parviflorus*
Very frequent severe drought	*L. laevigatum*	¬	*L. parviflorus*
No fires, no herbivores	*L. laevigatum*	+	*L. parviflorus*

Table 4. Suggested scenarios for oscillation of dominance between *Leptospermum laevigatum* and *Leucopogon parviflorus* in calcareous dune scrub, Norman Bay.

a scenario well documented by Hazard and Parsons (1977) at Western Port. However at both sites, the role played by *Allocasuarina verticillata* in the dynamics is not clear. Although at Norman Bay it occasionally regenerates from seed and root suckers, it does not appear likely to become a major species at that site - in marked contrast to the situation on some of the calcareous dunes on Yanakie Isthmus.

The oscillation of dominance of these two species may also be affected by drought, since *L parviflorus* may be more severely damaged than *L. laevigatum* and possibly killed. Following prolonged periods of drought therefore, the dominance of *L. laevigatum.* may increase.

In the Norman Bay area fire regimes would need to be delicately balanced to preserve the *status quo* of vegetation types. We know little of the past aboriginal activities in this area except that kitchen middens of shells and charcoal are common around the coastline. It seems likely therefore that coastal and sub-coastal communities were burnt more frequently than the inland slopes and mountain tops. Given the rapidity with which heathland is invaded and suppressed by *L. laevigatum* from the coast and by *Kunzea ambigua* from adjacent rocky outcrops, and given the ease with which both species are killed by fire (Judd 1986), it is not beyond the bounds of possibility that in the past much heathland was anthropologically maintained by fire frequency.

To conserve vegetation types we must know the controlling factors and we must decide what we want conserved. If nothing is done that is a management option; if we leave it to chance, that is also an option. If we want a certain type of dune scrub or a floristically rich heathland to remain as such, some intervention is necessary. To this extent conservation is frequently a value judgement. A scenario of factors affecting the dominance of overstorey in dune scrub is shown in Table 4.

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